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On the organization of ecosystems

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Chapter 1

General introduction

Michiel P. Veldhuis

Introduction

Ecosystems are currently under pressure all around the globe through changes in land-use, climate, nutrient depositions, atmospheric carbon dioxide levels and biodiversity, as a result of increased human populations and activities (Sala *et al.* 2000; Walther *et al.* 2002; Field & Van Aalst 2014). More importantly, this is expected to continue in the near future. Therefore, ecologists face the challenging task to understand and predict the effects of all these human-induced changes on ecosystems. Inevitably, a thorough understanding of ecosystem organization and functioning is needed to increase our predictive ability of ecosystem response to environmental changes.

Ecosystems organization

In ecosystems, organisms interact with each other and the environment, directly and indirectly, in many different ways, forming complex interaction networks (Gillson 2004; Pringle *et al.* 2010; Sterling, Gomez & Porzecanski 2010). Ecologists have traditionally sought to understand this overwhelming complexity and its evolution in a reductionist manner adopting a taxonomic approach. However, problems arise in attempts to draw useful generalizations about ecosystem organization and behavior by synthesizing results from studies with a species-centered approach. The recognition that dynamic systems can exhibit complex, non-linear, chaotic and self-organizing behavior that is not simply predictable from the properties of their basic building blocks (Levin 1999; Sole & Goodwin 2008) inspired scientists in other biological disciplines (biochemistry, cell biology, organismal physiology) to examine the organization of interactions in cells and organisms, rather than the characteristics of their isolated components (Rosen 1991; Kitano 2002; Sun & Becskei 2010). As a result of such interactions, emergent structural properties and behavior often arise at the focal level of organization (Levin 1998; Morowitz 2002). Biological examples of such emergent properties are bird flocking behavior and termites mound building, which are hard to predict from the characteristics of separate individuals, or problematically, from their DNA sequences. Nevertheless, both emergent properties can be described by simple rules of interactions between individuals through the process of self-organization (Camazine

2003). In analogue, a generally accepted concept that describes how “simple” interactions at the species level are structured and organized at the ecosystem level not yet exists, hampering our predictive ability of ecosystem responses to imposed threats. Furthermore, such a concept could provide a mechanistic understanding for the patterns and processes observed at the ecosystem level (nutrient cycling, bi-stable states, vegetation patterns).

African savanna ecosystems

Savannas are important ecosystems, both from an ecological and socio-economic perspective. They occupy a fifth of earth's land surface and contain a large and rapidly growing proportion of the world's human population and the majority of its rangelands and livestock (Scholes & Archer 1997). Furthermore, savanna ecosystems are expected to be very sensitive to future changes (Sala *et al.* 2000; Midgley & Bond 2015). Nevertheless, how they will be affected by human-induced environmental changes is poorly known.

Sub-Sahara African ecosystems are water-limited (Nemani *et al.* 2003; Sankaran *et al.* 2005), making these ecosystems sensitive to alterations in precipitation events. One of the primary consequences of climate change is a shift in precipitation patterns (Hulme *et al.* 2000), which is therefore expected to affect ecosystem structure and functioning. Nevertheless, savanna ecosystem structure is poorly predicted by climate alone (Lehmann *et al.* 2011), but is also dependent on the disturbance regime, such as regular fire outbreaks which ‘consume’ large parts of vegetation biomass (Bond & Keeley 2005; Staver, Archibald & Levin 2011a). Besides these fire disturbances, also other consumers like large herbivores (McNaughton 1984; Sankaran, Augustine & Ratnam 2013) and termites (Freyman & Olff 2009; Pringle *et al.* 2010; Sileshi *et al.* 2010) strongly affect ecosystem structure and functioning. The distribution of these consumers is strongly dependent on rainfall (Hempson *et al.* 2014). Furthermore, there are interactions between vegetation types (tree-grass interactions) (Scholes & Archer 1997), between groups of consumers (fire-grazer interactions) (Archibald *et al.* 2005) and functional groups of macrodetritivores (dung beetle-termite interactions) (Freyman & Olff 2009). Additionally, both vegetation and consumers might feedback on local environmental conditions by changing water and nutrient availabilities (Belsky *et al.* 1989; McNaughton, Banyikwa &

McNaughton 1997a; Bond & Keeley 2005; Sileshi *et al.* 2010). Altogether, this results in a very complex structure of interactions with many determinants and feedback mechanism. Not surprisingly, dynamic global vegetation models (DGVM's) are generally found poor predictors of savanna ecosystem structure and functioning (Bonan *et al.* 2003; Hely *et al.* 2006; Hickler *et al.* 2006; Sato, Itoh & Kohyama 2007). Therefore, a general concept based on the interactions between species that incorporates the feedback mechanisms is now needed to describe the organization of savanna ecosystems to subsequently explain the patterns that arise at the ecosystem level.

Objectives

With this dissertation, I aim to contribute to a better general understanding of ecosystem organization, with a special focus on African savanna ecosystems. To this end, I first review and further develop the concept of ecological autocatalysis, that combines information on consumer-resources linkages with additional feedback mechanisms to identify groups of organisms that positively affect each other (autocatalytic loops). Interactions between multiple autocatalytic loops can provide a mechanistic understanding of the patterns and processes found at the ecosystem level. Therefore, the concept of ecological autocatalysis could serve as a framework to understand ecosystem organization in any ecosystem. Subsequently, I explore how this concept might yield useful insights in the description of ecosystem organization of real ecosystems, using an African savanna as a study system. I first explore how biotic feedback mechanisms, that are central to the concept of ecological autocatalysis, can change local availabilities of water and nutrient, loosening the connection with large-scale environmental gradients. I then investigate the strength of consumer-resource linkages, that form the backbone of the autocatalytic loops, by quantifying the rates of primary production, herbivore consumption and decomposition across a rainfall gradient. Together, these consumer-resource linkages and the biotic feedback mechanisms, determine the strength of positive feedback within each loop and consequently, the negative interactions between the loops. Therefore, they provide the basis for the understanding of the importance of ecological autocatalysis for the organization of African savanna ecosystems.

Last, I investigate how these obtained insights in the organization of savanna ecosystems provide a mechanistic explanation for the vegetation patterns and spatial heterogeneity of the landscape.

Study area

All data for the studies in this thesis were collected in Hluhluwe-iMolozi Park, South Africa. Hluhluwe and Umfolozi game reserves were first proclaimed in 1895, and were connected by the so-called Corridor area in 1989 and now covers approximately 90.000 ha (Brooks & Macdonald 1983; Brooks 2005). The park is characterized by its high heterogeneity and covers a strong north south elevation gradient ranging from 584m to 38m, respectively. Mean annual rainfall ranges from approximately 500 to 900 mm, increasing with altitude (Balfour & Howison 2002). Wet season starts in October and ends in March. Annual mean temperature ranges from 13°C to 35°C, with higher temperature during the wet season. The parks vegetation is very heterogeneous with grazing lawns ranging between a few square meters to several of hectares that alternate with tall grasslands dominated by bunch/tussock forming species (Cromsigt & Olff 2008). Most abundant grazing lawn grass species are *Digitaria longiflora*, *Sporobolus nitens*, *Panicum coloratum*, *Urochloa mosambicensis*, *Dactyloctenium australe* and *Cynodon dactylon* and tall bunch grass communities are dominated by *Sporobolus pyramidalis*, *Themeda triandra*, *Eragrostis curvula*, *Panicum maximum*, *Digitaria eriantha*, *Setaria sphacelata*, *Cymbopogon excavatus*, *Hyparrhenia filipendula*, *Chloris gayana* and *Bothriochloa insculpta*. The geology of the park is complex and heterogeneous at small scales. Alluvial, dolerite, sandstone, shale and tillite parent material are present, resulting in soils ranging from very sandy to very clayey (King 1970).

The park hosts a variety and relatively high biomass of large herbivores (Waldram, Bond & Stock 2008; Cromsigt *et al.* 2009). The most important herbivores are African buffalo (*Syncerus caffer*), African elephant (*Loxodonta africana*), blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchellii*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), grey duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), warthog (*Phacochoerus africanus*) and white rhinoceros (*Ceratotherium simum*). The park is well-known for its high densities of rhino's and is one of the last areas

in the world with high densities of megaherbivores. Furthermore, it possesses spatial maps of burned areas for the last 60 years and a good logistic network. Altogether, the steep rainfall gradient, 'intact' herbivore assemblage, good vegetation maps, fire record and logistic network made this an ideal study site to address the objectives of this thesis.

Thesis outline

I start with a review on the concept of ecological autocatalysis (**Chapter 2**) that follows from key concepts in community ecology (interspecific interactions, community assembly, ecosystem engineering) and develop the framework further to link community processes to important ecosystem patterns and processes (nutrient cycling, alternative stable states, landscape heterogeneity). Subsequently, I apply this concept to African savanna ecosystems to investigate its practicality for the understanding of ecosystem organization. Therefore, I first investigate the biotic feedbacks on local availability of resources (i.e. water, nutrients) (Chapter 3,4 and 5), key to the concept of ecological autocatalysis. First, in **Chapter 3**, I investigate an alternative hypothesis on grazing lawn formation. Current literature focuses on effects of defoliation and nutrient cycling, but is unable to explain grazing lawn formation in all ecosystems. I added additional feedback mechanisms that decrease water availabilities in soils of heavily grazed patches, resulting in grazing adapted vegetation (lawn grasses). In **Chapter 4** I quantify how large grazers and macrodetritivores redistribute nutrients across the landscape, highlighting the important role of the megaherbivore white rhinoceros. Furthermore, I found that nutrient redistributions by animals within the system are significant and extensive and of the same order of magnitude as regional atmospheric nutrient in and outputs (emissions, fixation and deposition). In **Chapter 5** I investigated whether these localized biotic feedbacks outweigh a major regional rainfall gradient in determining the nutrient limitations of plants (using foliar N:P ratios). I indeed found that distinct vegetation types just several meters from each other differed strongly in N:P ratios, whereas N:P ratios did not change over a rainfall gradient, suggesting a strong biotic feedback. Then, I studied the strength of consumer-resource linkages that server as the basic interaction structure of the autocatalytic loops and eventually

determine how nutrient and energy cycle through ecosystems. Therefore, I quantified how important ecosystem fluxes, as primary production, herbivore consumption and organic matter decomposition, differed across the rainfall gradient and between vegetation types (Chapter 6 and 7). In **Chapter 6** I investigated the effect of rainfall, temperature and different decomposer communities (microbes, non-social macrodetritivores, termites) on organic matter decomposition. Microbes and non-social macrodetritivores decreased their activity in period with low water availability, whereas termites showed no effect. Therefore, termites decrease the dependence of the decomposition process on environmental variability, increasing robustness against climate change.

Last, I investigate how the obtained information about the organization of African savanna ecosystems in the previous chapters, using the concept of ecological autocatalysis, helps to explain the patterns in vegetation and spatial heterogeneity of the landscape (Chapter 7 and 8). In **Chapter 7**, I quantified the primary productivity and large herbivore consumption of both lawn and bunch grasslands across the rainfall gradient and concluded that the differences in primary productivity were more important than the differences in herbivore consumption in determining the spatial heterogeneity in vegetation height of the savanna grass layer. In **Chapter 8**, I analyzed the effect of rainfall, fire, grazers and browser on the spatial patterning of woody species across the landscape. I found that rainfall and fire both increase clustering of woody species and that the effect of herbivores is more complicated. The study suggests a switch from tree-tree competition for water under low rainfall conditions towards tree-tree facilitation through protection against fire under higher rainfall conditions.

The final chapter of the thesis (**Chapter 9**) integrates the results of the preceding chapters (3-8) with the current scientific literature and discusses how they fit into the framework presented in chapter 2. It describes how the understanding of African savanna ecosystems might benefit from the concept of ecological autocatalysis and identifies some promising avenues for future research.

